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Acacia saligna seed banks: Sampling methods and dynamics, Western Cape, South Africa

M. Strydom [a,*], K.J. Esler [a], A.R. Wood [b]

[a] *Department of Conservation Ecology and Entomology, Stellenbosch University, Matieland 7602, South Africa*
[b] *ARC-Plant Protection Research Institute, Private Bag X5017, Stellenbosch 7599, South Africa*

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Abstract

Acacia saligna is potentially the most damaging invasive species in the coastal lowlands of the south-western Cape. The gall rust fungus, *Uromycladium tepperianum*, has been highly successful as a biological control agent for *A. saligna* populations in South Africa and has effectively reduced density, canopy cover and seed production of the tree. However, concerns still remain about the soil-stored seed bank and knowledge of seed bank status and dynamics is crucial for effective management. This study evaluated the effectiveness of two different sampling methods in assessing the status of the seed bank, how the seed bank of *A. saligna* at two different sites varies over time and how these findings compare to findings of other seed bank studies of *A. saligna* across southern Africa. Even with the reduction in seed production caused by biological control, numbers of seed in the soil seed bank are high enough to maintain high levels of recruitment after management or natural disturbances. Both sampling methods (grid and random sampling) attempted were effective in assessing the vertical distribution of the seed bank and estimated the size of the seed bank to be within the same order of magnitude. However, random sampling is more effective in assessing seed bank size as it was found that the seed has a clumped horizontal distribution. The vertical distribution of seed in the seed bank was found to be influenced by soil properties. The largest portion of the seed bank is situated in the upper 10 cm of the soil profile and declines in size with depth.

Keywords: Invasive alien plant; Seed density; Spatial distribution; Techniques

1. Introduction

Introduced species endanger global biodiversity and ecosystem services (Mack et al., 2000; Higgins et al., 1999). Detrimental effects invasive alien species have on the natural environment include reduced species abundance and diversity, species extinctions and changes in nutrient cycling, water availability and fire regimes (D'Antonio and Vitousek, 1992; Mack et al., 2000; Maron and Connors, 1996; Richardson et al., 1992). The fynbos biome in South Africa, renowned for its high species richness (Bond and Goldblatt 1984; Goldblatt and Manning, 2000), is scourged by a whole range of invasive aliens of which *Acacia saligna* (Labill.) Wendl. (Port Jackson willow) is potentially the most damaging in the coastal lowlands of the south-western Cape (MacDonald and Jarman, 1984; Van Wilgen and Richardson, 1985).

Indigenous to south Western Australia, this small leguminous tree or shrub (Cronk and Fuller, 1995; Morris, 1987; Morris, 1991), was introduced to South Africa in the mid-nineteenth century to stabilize shifting sand dunes (Shaughnessy, 1980). *A. saligna*'s success as an invader can be ascribed to a pre-adaptation to a Mediterranean-type climate, a variety of soil types (frequently nutritionally poor) (Bell et al., 1993; Witkowski, 1991) and periodic fires (Bell et al., 1993). Consequently in the west, south

* Corresponding author.
E-mail address: strydomm@sun.ac.za (M. Strydom).

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and eastern coastal regions *A. saligna* has formed large dense stands over a vast area on conservation, water catchment and agricultural land (Morris, 1997, 1999). This has resulted in the replacement of natural vegetation, alterations in ecosystem processes and interference with agricultural practices (Morris, 1997, 1999).

In an effort to control the invasion, *Uromycladium tepperianum*, a gall inducing rust fungus, indigenous to Australia, was introduced into *A. saligna* populations in South Africa as a biological control agent. This was done after isolates obtained from *A. saligna* were demonstrated to be host specific (Morris, 1987) and were observed as having detrimental effects to the host plant in its native habitat (Morris, 1997, 1999). *U. tepperianum* has been highly successful as a bio-control agent as it has resulted in decreased stand density (5–10% of original tree density) (Morris, 1999), reduced canopy density and seed production (Wood and Morris, 2007). In addition a seed-feeding weevil, *Melanterius compactus*, was introduced into *A. saligna* populations in South Africa to compliment the impact of the gall inducing fungus and to reduce further the seed production levels of *A. saligna* (Wood and Morris, 2007).

Even with the highly detrimental effects of *U. tepperianum* on *A. saligna*, seed production is still high enough to lead to the accumulation of numerous viable seed in the seed bank and therefore may still be great enough to maintain high levels of recruitment, creating a cause for concern (Morris 1999). *A. saligna* seed is approximately 5–6 mm in length and 3–3.5 mm in width (Doran et al. 1997) and has an energy content of about 21,9 kg g^{-1} (King, 1976). Previous studies indicate that *A. saligna* seed maintains high levels of viability in the seed bank, 86.6% (Milton and Hall, 1981) and 86–100% (Holmes et al., 1987). The accumulation of large persistent seed banks in the soil is a consequence of *A. saligna*'s seed possessing water-impermeable testas allowing seed to remain dormant in the soil, ensuring their temporal and spatial survival (Holmes et al., 1987; Rolston, 1978). Seed dormancy is broken when the testa is sufficiently damaged to allow water absorption (Milton and Hall, 1981), a process generally initiated by a heat pulse (Jeffery et al., 1988; Tran and Cavanagh, 1984).

A. saligna's soil stored seed banks vary in size and are determined by a large number of different factors including seed rain, the age of the stand, stand density or canopy cover, distance from canopy (Richardson and Kluge, 2008), duration of seed dormancy, predation, decay (Milton and Hall, 1981; Weaver and Cavers, 1979), substrate type and degree of soil disturbance (Holmes and Cowling, 1997). The rate of seed accumulation increases with tree age until the trees reach an age of approximately 30 years where after seed accumulation rate stabilizes (Milton and Hall, 1981). The seed banks of *A. saligna* in southern Africa have been recorded as being between 2000 seeds/m^2 (Morris, 1999) and 212,000 seeds/m^2 (Morris, 1997).

The distribution of seed in the soil profile is influenced by dispersal vectors (e.g. ants and water), soil organisms (e.g. mole rats), substrate type (Milton and Hall, 1981), percolation of water and openings left in the soil for example by decomposing roots (Harper, 1977). *A. saligna* seeds are located primarily in the top 8 cm of the soil profile and the seed density has been found to decline rapidly below this level (Milton and Hall, 1981). The nature of the soil will determine how deep seed penetrates into the substrate (Milton and Hall, 1981; Richardson and Kluge, 2008), with seed having been located at a depth of 35 cm in loose sandy soil (Milton and Hall, 1981) and 80 cm in riparian soils (Esler and Boucher, 2004). It has been concluded that horizontal dispersal of Australian acacias is even in southern Africa (Milton and Hall, 1981), while seed of *Acacia* species tends to have a clumped distribution in Australian soils which is attributed to storage of seed by ants in their nests (Majer, 1978). Thus seed density is largest under the canopy of the trees and declines rapidly when moving away from the canopy (Milton and Hall, 1981).

Knowledge of seed bank status and dynamics is crucial for effective management of *A. saligna* and this study contributes to the understanding thereof through:

1. Testing the effectiveness of different sampling methods in assessing the seed bank of *A. saligna*.
2. Evaluating how the seed bank of *A. saligna* at two different sites varies over space and time.
3. Comparing the findings of the two sites to findings of other seed bank studies of *A. saligna* across southern Africa.

2. Methods

Data were collected from two sites, Swartwater and Burgerspos (Table 1) at two sample dates — April 2009 (post-dehiscence) and September 2009 (pre-dehiscence).

2.1. Data collected during April 2009 (post-dehiscence)

At both sites one 625 m^2 plot was selected in an area with a closed canopy dominated by the target species. In the plot, a grid was established, consisting of five horizontal rows spaced 5 m from each other and five vertical rows spaced 5 m from each other. At every point where the horizontal and vertical lines crossed, a soil sample was taken, giving a total of 25 samples per site.

Soil samples were acquired using a rectangular metal pipe 51.6 cm long and 5 cm wide. The pipe was divided into 5 segments (each 10 cm long, volume of one segment = 0.00025 m^3), separated by 0.4 cm grooves cut horizontally into the pipe. Soil samples were taken to a depth of 40 cm as Esler and Boucher (2004) found the seed of *A. saligna* to be primarily located in the top 0–40 cm of the soil profile. After the soil corer was extracted from the soil, metal plates were inserted into the grooves, dividing the soil in the corer into 4 depth classes: 0–10 cm, 10–20 cm, 20–30 cm and 30–40 cm. The soil of every sample from each depth class was sieved through a 2 mm mesh and the seed counted. The average number of seed for every depth class was calculated. Seed viability was not tested as previous studies (Holmes et al., 1987; Milton and Hall, 1981; Strydom unpublished data) assessed most of the seed to be viable. Data from the two sites for the 0–10 cm depth class were tested for normality and either subjected to a one way

Table 1
The location and general characteristics of the study sites Swartwater and Burgerspos.

Site	Location	History of invasion	Vegetation type	General soil type	Gall rust fungus introduction	Tree density/m^2	Soil penetrability
Swartwater	S 33° 17′ E 18° 16′	>20 years	Swartland Granite Renosterveld [a]	Coarse sandy to loamy soils [a]	1988 [b]	2.26±0.57	71.5±9.62
Burgerspos	S 33° 31′ E 18° 32′	>20 years	Atlantis Sand Fynbos [a]	Grey regic sands [a]	1989 [b]	2.01±0.50	69.2±12.30

[a] Vegetation and general soil type as described by Rebelo et al. (2006).
[b] From Morris (1997).

ANOVA and/or a Mann–Whitney *U* test depending on the parametric or nonparametric nature of the data.

Data of the 0–10 cm and 10–20 cm depth classes were tested for spatial autocorrelation using Moran's I and Geary's C statistical tests. Moran's I values range from −1 to +1 with −1 indicating even dispersion, 0 random dispersion and +1 clumped dispersion. Geary's C values range from 0 to 2 with 1 indicating random dispersion, <1 clumped dispersion and >1 even dispersion. Spatial autocorrelation tests were only applied to these depth classes as other classes contained too little data to apply meaningful statistics. Furthermore the effect size was calculated to determine the number of samples required to accurately assess the status of the seed bank at different sites.

2.2. Data collected during September 2009 (pre-dehiscence)

A second set of data were collected during the last week of September 2009 using a different sampling technique. This was done as the effect size derived from data collected during April 2009 (Fig. 1) indicated a larger number of independent (i.e. not spatially correlated) samples were needed to accurately assess the status of the seed bank. Independent samples are required since results from the first set of samples showed the distribution of seed in the top soil layer, where most of the seeds are situated, to be clumped. Random sampling is therefore needed to negate the effect of seed aggregation on seed bank data.

A soil corer as described above was used to sample the seed bank during September. Thirty samples were taken at each site at random locations within the *A. saligna* stands. A random number table was used to determine the number of steps (>10 m) and direction of movement between samples. Samples were taken with a soil corer to a depth of 20 cm and were divided into 10 cm and 20 cm depth classes. The soil was sieved through a 2 mm mesh and the seed counted. The average number of seed at each depth for both sites was calculated. Data from the two sites were tested for normality and either subjected to a one way ANOVA and/or a Mann–Whitney *U* test depending on the parametric or nonparametric nature of the data.

At both sites, density of *A. saligna* was determined by counting the number of trees within five randomly placed 5 × 5 m plots and calculating the average. The plots were randomly distributed using the same procedure as above. Furthermore tree density data were tested for normality and either subjected to a one way ANOVA and/or a Mann–Whitney *U* test depending on the parametric or nonparametric nature of the data.

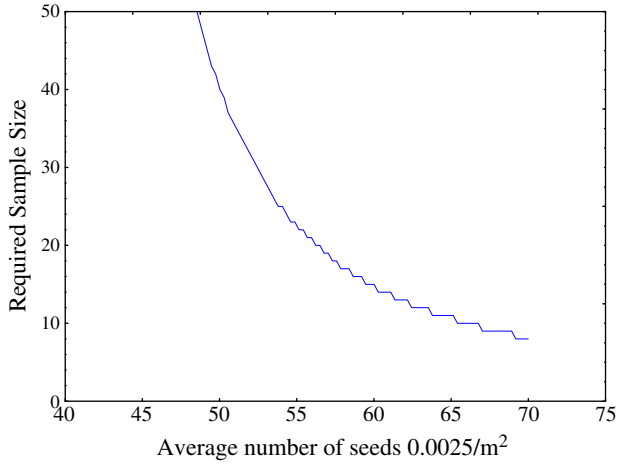

Fig. 1. Indicates the effect size which dictates the number of samples required to accurately assess the status of the seed bank for an area. The figure suggests that between 30 and 50 samples are needed to detect significant differences between the sites sampled in this study [however 30 samples did not detect differences between sites in the second sampling event in September 2009].

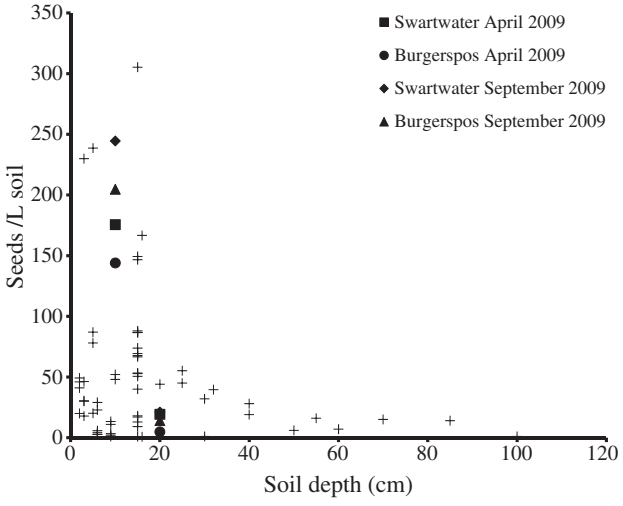

Fig. 2. Indicates the vertical distribution of *Acacia saligna* seeds/L soil in the soil at different sites with different vegetation cover and invasion histories. (Data indicated in bold symbols are from this study, additional data were sourced from various other studies listed in Appendix I).

As a proxy for soil depth, relative soil penetrability was assessed by hitting a metal stake (1.5 cm thick) as far as possible into the ground, the distance the stake moved into the earth was measured. This was repeated ten times at every site, and the average depth calculated. These data were tested for normality and either subjected to a one way ANOVA and/or a Mann–Whitney *U* test depending on the parametric or nonparametric nature of the data.

In order to convert data from this study and other studies to number of seed per litre for comparison purposes (as shown in Fig. 2), the following formula was used $V=(x\pi r^2/\pi r^2 h)/1000$ for data obtained with a cylindrical shaped corer, and for data sampled with a rectangular shaped corer $V=(xl^2/l^2h)/1000$. Where V = number of seed per litre; x = seed per m^2; r = radius of the soil core; h = depth of soil core; l = width of soil core.

3. Results

3.1. Site characteristics

The density of *A. saligna* trees at Swartwater is slightly higher than at Burgerspos (Table 1), however, the difference in density between these sites was not significant (ANOVA p-value = 0.49). Furthermore the relative penetrability of the soil at Swartwater is greater than at Burgerspos, although the difference is not significant (ANOVA p-value = 0.49).

3.2. Seed bank size and vertical seed distribution

When compared to Burgerspos, Swartwater had the largest number of *A. saligna* seed m^{-2} in each depth class for both months sampled (Table 2). However, differences between the 0–10 cm depth class for both methods in each month were not significant (ANOVA p-value = 0.37 for April 2009, and = 0.22 for September 2009).

Swartwater had a wider vertical seed distribution range than Burgerspos, with Burgerspos having no seed at depths deeper than 20 cm from the soil surface. Furthermore, for both months and sites the largest number of seed was located in the top 0–10 cm of the soil profile.

3.3. Horizontal seed distribution

The Moran's I values (April data, Table 3) for the 0–10 cm depth class were 0.211 and 0.106 for Swartwater and Burgerspos respectively, indicating a clumped distribution pattern for seed in the soil in this depth class at both sites. However, only the Moran's I value of Swartwater (p = 0.0098) was found to be significant. The clumped distribution pattern in the 0–10 cm depth class at both sites is further supported by the Geary's C values (Table 3) which were 0.75 for Swartwater and 0.85 for Burgerspos. However, the Geary's C value for both sites for the 0–10 cm depth class was not significant.

Table 3
Moran's I and Geary's C autocorrelation values for Swartwater and Burgerspos (April 2009).

Site	Depth	Statistic method	Value for Moran's I or Geary's C	p-value
Swartwater	0–10	Moran's I	0.211	0.010
		Geary's C	0.750	0.012
Swartwater	10–20	Moran's I	−0.074	0.747
		Geary's C	1.243	0.952
Burgerspos	0–10	Moran's I	0.106	0.077
		Geary's C	0.851	0.095
Burgerspos	10–20	Moran's I	−0.062	0.578
		Geary's C	0.977	0.420

The Moran's I and Geary's C spatial autocorrelation values (Table 3) for both Swartwater (−0.074 and 1.243) and Burgerspos (−0.062 and 0.977) for the 10–20 cm depth class indicate that seeds are randomly distributed within this depth class. However, both the Moran's I and Geary's C values for the 10–20 cm depth class were not significant. The 20–30 cm and 30–40 cm depth classes were not tested with Moran's I and Geary's C tests for spatial autocorrelation as too little seed was present in these depth classes to do meaningful analyses.

3.4. Sampling methods

Samples acquired during April 2009 were taken post dehiscence whereas samples acquired during September 2009 were sampled pre-dehiscence, yet the average number of seed obtained was substantially larger using the random rather than the grid sampling method at both sites. While different methods were used to retrieve seed from the soil profile in April and September 2009, both methods still indicated that most seeds are located in the top 0–10 cm of the soil and the number of seed decreases as one samples deeper into the soil profile at both sites. However, the standard deviation as a proportion of the mean increased for the random sampling method at both sites for the 0–10 cm depth

Table 2
Average number (±S.D.) of *Acacia saligna* seeds m^{-2} from different soil profile depths at Swartwater and Burgerspos in April and September 2009.

Site	Month	Sampling method	0–10 cm	10–20 cm	20–30 cm	30–40 cm
Swartwater	April	Grid	17,552±9681	1920±4387	144±488	48±132
Burgerspos	April	Grid	14,400±8044	480±632	0±0	0±0
Swartwater	September	Random	24,452±19,676	2108±3408	ND	ND
Burgerspos	September	Random	20,468±14,628	1400±3392	ND	ND

First number indicates average number of seeds/m^2; second number indicates standard deviation.
ND = No Data.

and at Burgerspos for the 10–20 cm depth. Furthermore the ratios of seed found between Swartwater and Burgerspos remained approximately the same for both sampling methods, these were 1:1.22 and 1:1.19 (Swartwater:Burgerspos) for the grid and random sampling methods respectively.

4. Discussion

To obtain accurate estimates of seed densities of invasive *A. saligna*, two sampling methods for seed banks were compared, providing a basis for future studies. Invasive *A. saligna* presents serious challenges for managers, as significant numbers of seed are still present in upper soil layers, despite the 20 year presence of a destructive biological control agent.

4.1. Grid vs random sampling

The grid sampling method samples seed in a small area relative to the overall above-ground cover of the *A. saligna* stand. The average seed per unit area is calculated and extrapolated to represent the seed bank status of the whole stand. The problem with this method is it can miss subtle spatial variation in the seed bank arising for example due to differences in soil profile or in the age of the trees present in the stand (Benoit et al., 1992; Gross, 1990). This can be rectified through increasing the size and number of grid used in the area (Bigwood and Inouye, 1988). A clumped distribution was found for seed in the upper 10 cm of the soil (Table 3). Thus it is possible that aggregations of seed were sampled more than once, this is undesirable as this will lead to over- or under-estimation of the seed bank size (Bigwood and Inouye, 1988; Wiles and Schweizer, 2002). Furthermore, sampling seed banks is a tedious process (Ambrosio et al., 2004; Benoit et al., 1992; Wiles and Schweizer, 2002) and increasing the size of the grids to be sampled dramatically increases the time spent sampling. This method is still effective to attain data on the vertical and horizontal distribution of seed in the seed bank if the grid or grids are representative of the area and if the sample size is adequate. When testing for spatial autocorrelation this method has to be used (Wiles and Schweizer, 2002).

The random sampling method consists of sampling at different, random located points within an area covered by *A. saligna* trees. The average seed per unit area is calculated and assumed to represent the status of the seed bank for the whole area. This method has a higher probability of incorporating horizontal variation in the seed bank as it covers a larger area and also avoids regularly sampling the same aggregation of seed (and therefore over- or under-estimating the seed bank size). Therefore when a clumped spatial pattern is present this sampling method will give a more accurate indication of the seed bank size, but cannot be used to determine any spatial pattern (Wiles and Schweizer, 2002). As this method covers a larger area, the technique requires more samples to be taken. However, the number of samples needed to increase the random sampling techniques' accuracy in determining the size and variation of the seed bank is still less than the number required by the grid sampling method.

This study revealed that, even though the sites varied in habitat characteristics and density of invasion, there were no significant differences in seed bank sizes between sites. However, random sampling revealed larger seed banks with greater variability for both sites than the grid method and therefore random sampling provides a more accurate sampling method to determine seed bank size across entire stands. The seed bank was expected to decline from April (pre-dehiscence) to September (post-dehiscence) due to predation, germination etc. That the opposite was obtained further supports the argument that the former technique is the more accurate method. It may also be possible that within unevenly aged and distributed stands the spatial variation increases.

4.2. Seed bank dynamics in Swartwater and Burgerspos

The current seed bank status of Swartwater and Burgerspos in the top 0–10 cm of the soil for April respectively is comparable to previously published data for these sites (Morris 1997), and confirms previously published data that the majority of seeds are located in the upper part of the soil profile (Holmes, 2002; Milton and Hall, 1981). Morris (1997) bulked 10 samples taken with a soil corer to 15 cm depth at 1 m intervals along each of four close by transects, during April/May, this methodology is comparable to the April 2009 sampling. The seed bank at Swartwater increased significantly in size since 1996 (Table 4). In contrast, the seed bank at Burgerspos showed a trend of decline; however this trend was not significant.

The reason *A. saligna* seed can be found at greater depths at Swartwater than at Burgerspos can be ascribed to the soil of Swartwater having a sandier texture (Milton and Hall, 1981).

Table 4
Average number (±S.D.) of *Acacia saligna* seeds m^{-2} at a depth of 15 cm for Swartwater and Burgerspos (data from Morris, 1997). Years when fires occurred, prior to monitoring, are indicated by grey shading, with little impact on seed bank.

Site	Year							
	1991	1992	1993	1994	1995	1996	2009	
Swartwater	3000 ± 1500*	6000 ± 2600	5000 ± 1600	7000 ± 1100	16000 ± 1100	8000 ± 3600	17552 ± 9681	24452 ± 19676
Burgerspos	22000 ± 5100	33000 ± 11000	17000 ± 4900	15000 ± 1300	18000 ± 7200	22000 ± 9800	14400 ± 8044	20468 ± 14628

First number indicates average number of seeds/m^2; second number indicates standard deviation.
First column of 2009 indicates data collected during April 2009.
Second column of 2009 indicates data collected during September 2009.
*S.D. data from Morris (1997) has n=4 (each of 10 bulked cores), 2009 data has n=30.

Decay rates for the seed at Burgerspos reaching soil depths deeper than 20 cm in the soil can also possibly be higher as the water table during winter is very near the soil surface (Personal observation). Furthermore the greater vertical distribution of seed at Swartwater may also be a result of more intense soil organism activity (such as by dune mole rats) or soil disturbance, as has been found in previous research (Holmes, 2002; Milton and Hall, 1981; Weaver and Cavers, 1979). Seedlings of other Australian Acacias, similar to *A. saligna* in having seed of comparable size, fail to reach the soil surface and/or are unlikely to establish when germinating below a depth of 10 cm (Pieterse, 1997). However, dormant seed deeper in the soil profile may be moved by soil organisms (Milton and Hall, 1981) to a position within the profile where they are able to emerge if their germination cues are met.

The clumped distribution of seed in the top 0–10 cm of the soil at both sites can be because ants store the seeds in their nests (Holmes, 1990; Milton and Hall, 1981), or possibly because the trees in the area are not uniformly distributed (Benoit et al., 1992; Holmes et al., 1987; Milton and Hall, 1981), or due to the uneven soil surface profile wherein seed accumulates in small dips. The reason for the random distribution of the seed below 10 cm in the soil profile can possibly be because seed movement from the top soil layer is difficult as the soil resistance increases and the fine roots of the trees and other vegetation in this area prevent or decrease the rate of downward movement in the soil. Therefore seed movement is stochastic and can be attributed to the random weakening of one of the factors preventing downward movement in the soil or the random disturbance of these seed aggregations by soil organisms.

There is a trend evident for *A. saligna* stands that indicate, despite different vegetation cover, soil properties and invasion histories, seed banks of *A. saligna* tend to decline in size with depth and the largest portion of the seed banks are situated in the upper 10 cm of the soil (Fig. 2).

5. Conclusions

Depending on the required goal of a study, random sampling is possibly the most feasible method for sampling the seed bank as it yields reliable data that are not spatially autocorrelated. Seed banks of *A. saligna* remain a challenge for managers despite the reduction in seed production caused by biological control. Despite different vegetation cover, soil properties and invasion histories, the largest portion of the seed bank is situated in the upper 0–10 cm of the soil and the seed bank declines in size with depth.

Management/conservation implications

Despite biological control being present at the study sites for the past 21 years, seed banks are still large and have either increased or remained stable and therefore pose a serious management challenge. This suggests that a single clearing event will not be sufficient for control, and that budgets need to include aspects of managing the seed bank. *A saligna* management will be a long-term commitment.

Soil movement by earthworms and fossorial diggers (e.g. mole rats) will exacerbate this problem by continuous movement of seeds into the deeper soil profile. Although not massive, the seed bank in these deeper layers could be brought to the surface to re-establish *A. saligna* populations.

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Appendix I. Information describing locality, methods, data points and data sources used in Fig. 2

Location	Habitat	Treatment	Data collection	Seed/L soil	Source
NA	Riparian, deep sands	Mature, dense, un-burnt stand	1 L of soil bulked from N=4 samples; collected to depth of 100 cm	46; 78; 52; 45; 19; 16; 15; 14; 1	Boucher and Mortimer (2000)
NA	Wetland, sandy	Mature, dense, un-burnt stand, subject to 10 yrs biological control	4 bulked samples from 3, 2×2 m quadrats to a depth of 60 cm	87; 48; 44; 32; 28; 6; 7	Boucher and Fleitmann (2001)
Noordhoek	Wetland, deep sands	Mature, dense, un-burnt stand	30, 5×15 cm soil cores taken at each depth to a depth of 30 cm	41; 17; 1	Jasson and Esler (2003)
Simonstown	Shallow soils on Table Mountain Group	Previously dense, un-burnt stand, cleared and biomass stacked	30, 5×15 cm soil cores taken at each depth to a depth of 30 cm	13	Jasson and Esler (2003)

(*continued on next page*)

Appendix I (*continued*)

Location	Habitat	Treatment	Data collection	Seed/L soil	Source
Marina da Gama	Cape flats dune strandveld, soils with a sandy texture	Natural site, short invasion history, Thicket	50, 75×150 cm soil cores were taken	0.97	Milton and Hall (1981)
Stellenbosch	Clay soil	1 tree,	0.25 m^2 pit 5 cm deep	238.64	Milton and Hall (1981)
University of Cape Town	Cape flats dune strandveld, soils with a sandy texture	Cleared and burned	100, 75×150 cm soil cores were taken	17.96	Milton and Hall (1981)
Maitland Cemetery	Cape flats dune strandveld, soils with a sandy texture	Covered with grass, 100 yr recurrent thicket	0.25 m^2 pit 16 cm deep	0.675	Milton and Hall (1981)
Penhill	Swartland granite Renosterveld, rock with limited soils	Long history of invasion, cleared	50, 75×150 cm soil cores were taken	67.68	Milton and Hall (1981)
Faure	Swartland granite Renosterveld, Soils with a marked clay accumulation	Old thicket, history of invasion	50, 75×150 cm soil cores were taken	50.57	Milton and Hall (1981)
Penhill	Sand plain fynbos, Deep recent sands	Mature, felled and unburnt	20–60, 5×15 cm soil cores taken to a depth of 15 cm	69.33	Holmes et al.(1987)
Grootphisante-kraal	Renosterveld, Clays on Malmesbury shale	Mature, felled and un-burnt	20–60, 5×15 cm soil cores taken to a depth of 15 cm	305.33	Holmes et al.(1987)
Schustersrivier	Strandveld/mountain fynbos, Deep recent sands	Mature, felled, pile and burnt piles	20–60, 5×15 cm soil cores taken to a depth of 15 cm	88.00	Holmes et al.(1987)
Silvermine Nature Reserve	Mesic mountain fynbos, Shallow sand over sandstone	Mature, felled and burnt	20–60, 5×15 cm soil cores taken to a depth of 15 cm	52.80	Holmes et al.(1987)
Cape Flats Nature Reserve	Strandveld/sand plain fynbos mosaic, Deep recent sands	Mature, felled and burnt	20–60, 5×15 cm soil cores taken to a depth of 15 cm	149.33	Holmes et al.(1987)
Coppul	Agulhas limestone fynbos, Greyish, sandy excessively drained soils	Small trees	10, 7×15 cm soil core taken to a depth of 15 cm	86.67	Morris (1997)
Swartwater	Swartland Granite Renosterveld, coarse sandy to loamy soils	Small trees	10, 7×15 cm soil core taken to a depth of 15 cm	53.33	Morris (1997)
Kanonkop	Atlantis sand fynbos, Soils with a marked clay accumulation,	Small trees	10, 7×15 cm soil core taken to a depth of 15 cm	66.67	Morris (1997)
Riverlands	Atlantis sand fynbos, Soils with a marked clay accumulation	Small trees, burned during summers of 1992/1993 and 1993/1994	10, 7×15 cm soil core taken to a depth of 15 cm	40.00	Morris (1997)
Hutch's Place	Peninsula sandstone fynbos, rock with limited soils	Small trees	10, 7×15 cm soil core taken to a depth of 15 cm	86.67	Morris (1997)
Burgerspos (Dense)	Atlantis Sand Fynbos, Grey regic sands	Large trees, burned during summers of 1992/1993	10, 7×15 cm soil core taken to a depth of 15 cm	146.67	Morris (1997)
Burgerspos (Riverine)	Atlantis Sand Fynbos, Grey regic sands	Large trees, burned during summers of 1994/1995	10, 7×15 cm soil core taken to a depth of 15 cm	166.67	Morris (1997)
Mamre	Sand plain proteoid fynbos, Quaternary sand 400	Recently invaded, Dense, Un-burnt	Sampling frame, 15×15 cm and 5 cm deep. 20 samples taken at three depth levels of 3 cm each	49.17; 20.13; 5.77	Holmes (2002)
Pella	Sand plain proteoid fynbos, Quaternary sand 400	Recently invaded, Dense, Un-burnt	Sampling frame, 15×15 cm and 5 cm deep. 20 samples taken at three depth levels of 3 cm each	29.93; 22.80; 13.33	Holmes (2002)
Silvermine	Mountain proteoid fynbos, Colluvial sandy loam 700	Recently invaded and long invaded sites, Dense, Un-burnt	Sampling frame, 15×15 cm and 5 cm deep. 20 samples taken at three depth levels of 3 cm each	46.23; 4.13; 2.07	Holmes (2002)
Simonstown	Mountain proteoid fynbos, Colluvial sandy loam 700	Recently invaded and long invaded sites, Dense, Un-burnt	Sampling frame, 15×15 cm and 5 cm deep. 20 samples taken at three depth levels of 3 cm each	17.77; 2.80; 3.27	Holmes (2002)

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